THE ANATOMY OF MEGALODONTA BECKII.

BY A. V. HOECK.

Owing to the abundance of material found during the past vacation at Bankson Lake, Cass Co., Mich., as also because of the unique character of the plant itself as a submerged composite, it was considered possible that the anatomical study of *Megaladonta Beckii* (Torrey) Greene would show some interesting features structurally. The following notes are the result of the investigation of the plant, which is rather abundant in the places where it is found, but has not been reported from many localities in our region.

The plant was first discovered by Dr. Lewis C. Beck in Schuyler's Lake near Schenectady, N. Y. It was published by Torrey who referred it to the genus *Bidens* as *Bidens Beckii* in 1821.[1] Dr. E. L. Greene[2] raised the plant to generic standing as type of his new genus *Megalodonta*. He published at the same time a second species *M. nudata* from the Adirondacks, and another species from Greene Lake, Washington. As characteristic distinctions from the genus *Bidens* is mentioned especially the singular peculiarity not only among the *Bidentideae* as a group but even of the whole composite family, aquatic habit with submersed and dissected foliage not so much different in appearance from that of *Batrachium* (*Ranunculus*) *aquatile* (Linn.) Wimm[3]. of the old world or our own *Batrachium trichophyllum* Chaix) Bosch.[4] The flowers both ray and disk are peculiar. The rays are "retuse and notched instead of obtuse and entire." "The disk corollas are slender and clavate." "The achenes with their not at all compressed or angled but almost terete body surmounted by several long stout persistent awns of great size and prominence in relation to the essential part the fruit"[5] are the other characters of note. The generic name of the plant is derived from the Greek

[1] Torrey, J. in Spreng. Neue Entdeck., 2, p. 135 (1821) also Torrey, J., Flora of New York, 1, p. 388, pl. 68, (1843), Torrey, J., Compend. p. 312 (1826)) Spreng. Syst. 3, p. 455, (1826), Beck, L. C., Botany, p. 207 (1833) p. 191 (1848).

[2] Greene, E. L., Pittonia, 4, p. 271 (1901).

[3] Wimm. Fl. Schles. p. 8(1841).

[4] Bossch, Prod. Fl. Bat., p. 5 (1850).

[5] Greene, l. c.

μέγας, μέγαλος (megas, megalos) great, large and ὀδούς, ὀδόντος, (odous, odontos) tooth.

The plants used for study were found submerged in both Bankson and North Bankson Lakes in bloom during the latter part of August and the early part of September. The submerged leaves are opposite or whorled in 3's, and finely repeatedly dissected on the palmate plan. The emersed leaves two or three pairs in number are narrowly lanceolate to oblong and laciniately toothed, pinnate and reticulately veined. The lower emersed or intermediate leaves are often more or less deeply lobed or cleft appearing as transition forms from the aquatic to the aërial forms. The aquatic foliage invariably withers when by design or accident exposed even for a short time to the air though the emersed may for a rather long time remain undecayed when submerged. The plant grows in rather deep water from several decimeters to several meters, the lower stem or rhizome rooting below the mud level. The submerged floating stem and the aerial part are rather similar in structure and have large air cavities in the cortical region as also in single large central air space in the pith. The rihzome rooting below in the mud is devoid of this central air space and the cortical spaces are smaller and fewer. The adventitious roots at the nodes, even on the floating stem, and the upper roots are conspicuously green with chlorophyll. These roots reach down several decimeters or over a meter and when reaching the muddy bottom branch into numerous smaller divisions. The part of the stem creeping in the mud is not much over half the diameter of the floating aquatic stem, or about 2 mm. and sometimes less. The aquatic foliage is nearly as persistent as that of *Cabomba* but not as deciduous as that of *Neobeckia*. (*Roripa* or *Nasturtium aquatium*). A rather poor drawing of the plant is found in Torrey's Flora of New York already cited and one somewhat better perhaps in Britton and Brown's Flora, both editions pp. 440 and 500 respectively. The characters of the plant may be had in the works cited as also from our common manuals more or less incompletely.

THE ROOT.

The young root has a well marked stele surrounded with well defined endodermis limiting the periblem (Fig. 1). The cell structure of the epiblema seems in no particular way different from that of the

epidermis of the stem. As a rule even in the older roots there is but one series of intercellular spaces more or less oblong and irregular in the cortex and with their ends pointing to the outside and inwards to the stele or anticlinaly while in the stems they are periclinal (Fig. 1a). Only one series of the larger spaces are found in the root and several in the stem, though in the former a few smaller ones are occasionally met with (Fig. 1b). Only one to three layers of cells are found between the larger spaces and the stele inclusive of the endodermis. The cortex of the larger adventitious roots (which were the only ones found for study) has a large number of chlorophyll grains even as far inwards as the endodermis excluded. Nor is chlorophyll found in either the epiblema or the palisaded hypodermal layer of the older roots (Fig. 2). The stele has a wood bundle of the radial type and the xylem is exarch pentarch, the phloem alternating with the xylem rays. Just outside of each phloem strand is a latex tube containing a brownish somewhat resinous substance. The tube is surrounded in this case by four secreting cells in the older roots (Fig. 3) though in young specimens these are not as yet well differentiated or developed These latex tubes are rather straight mostly unbranched tubes with four secretion cells around them (Fig. 3) and are found throughout the plant, and in the stem the secretion cells are more than four, usually about six. (Figs. 5, 8, 9, 13, 17). The pericycle is rather well differentiated as a marked layer of medium sized cells in young parts of the roots, but later it loses to some extent its characteristic appearance the cells of the cortex seeming to pass by gradual variations of size to those of the stele. Very little secondary change takes place in the stele especial in the xylem (hadrome) portion thereof; the ducts always are few in number as would be expected in this case because of the needlessness of these water conducting vessels in aquatic plants. The larger vessels formed later as metaxylem or perhaps secondary xylem are scalariform pitted, those of the protoxylem are annular and later spiral transitional to pitted. Longitudinal section of the root shows the peculiar variations of the tissues in the root in a marked way (Fig. 4). From the exterior we have in order the outer layer of cells (a) and the hypodermal layer (b) these two both devoid of chlorophyll. The cortical cells on both sides of the large intercellular spaces resemble one another, and bear chlorophyll in larger or smaller quantity depending on the exposure

to light. The section shown was made somewhat obliquely through the organ, showing several layers of cells of the tissue connecting the outer layers with the inner near the endodermis (f). In older roots six or seven of the cells in the outer part of the phloem acquire thickened walls though the thickening is never considerable. They seem to approximate to a schlerenchymatous nature, but scarcely typical stereome. Though there is now much difference between the outer layer of the stem and that of the young root, that of the latter with age is strikingly angled and the layer immediately under the epidermis has the appearance of palisaded cells, both layers being devoid of chlorophyll. That this layer may have arisen by subsequent periclinal division is not improbable but was not definitely determined (Fig. 2).

The pith of the root is devoid of intercellular spaces as found in the cortex.

RHIZOME.

While there does not seem to be any considerable difference in structure between the emersed and the submersed part of the stem, there is considerable variation between these and that part of the plant axis which creeps and roots under the mud and may be designated as the rhizome. This is never proportionately as thick and to the naked eye or under a common lens has an internally different structure, being devoid of the central intercellular space, while the cortical spaces are fewer and smaller. (Fig. 6 and 7). The fibrovascular bundles are of the collateral open type and the xylem is strictly pentrach and endarch (Fig. 5 and 6). The cambium forms a rather perfect circle in cross section, developing interiorly somewhat bricklike cells in the interfascicular part (medullary rays), the cells inwards passing gradually into those of the pith. These cells are much in appearance like the cells of the bundle and are thickwalled. The ducts in each bundle are in several series instead of only one as in the rest of the stem. On the outer part of the phloem there are a few layers of schlerenchyma fibres and just outside in the cortex an occasional latex tube. The interfascicular cambium dips inwards but little.

THE STEM PROPER.

The differences between the stem proper and the creeping rhizome have been noted already. The intrastelar fundamental

tissue (medullary rays) are so far extended into the cortical region that the interfascicular cambium is nearer to the epidermis than the outermost portions of the phloem, in spite of the fact that the bundles are open (?) collateral of the typical kind and the xylem endarch pentarch. (Figs. 7 and 8). Several layers within the epidermis there appear at regular intervals perfectly straight vertical latex tubes and near the fibrovascular bundles a few are found at irregular intervals. The xylem is wedge shaped and has outside of it oval strands of phloem, the latter with stereome in several layers on its outer margin. The protoxylem has the usual annular ducts which gradually pass into spiral and finally scalariform pitted, and the ducts in each bundle are all arranged in one line or series increasing in size outwards towards the surface of the plant. The centre of the stem or pith is occupied with a large hollow space.

LEAVES.

As already intimated there are two kinds of leaves present, the submersed and the emersed. The former are short petioled or nearly sessile and repeatedly palmately dissected into linear divisions which in structure are of the centric type. (Fig. 9). The epidermis which is scarcely differentiated except in size and lack of cellwall markings, bears chlorophyll like the rest of the mesophyll layers. Only the layers of cells immediately bordering on the vascular system are devoid of it. The cells of the mesophyll are polygonal in cross section and their sides are marked transversely with scalariform markings. (Fig. 10). The wood bundle is very simple and varies according to the distance the section is made from the petiole. Fig. 9 shows a cross section made of one of the divisions about the middle of the leaf, several ducts are present as also a latex tube as are phloem elements and wood parenchyma. The bundles of the larger and lower divisions are more typically open collateral (Fig. 11). Both xylem and phloem are rather well developed, the former rather more so than were expected in aquatic plants. The epidermis of the submersed leaves is of course totally devoid of stomata and the cells are somewhat longer than broad. (Fig. 12). The petiole of the aquatic leaf is rather more flattened than any of the divisions but it has only a single larger bundle not essentially different from the collateral bundle of the divisions. The phloem strand is rather extensive

in area and number of elements. (Fig. 13). Calcium oxalate crystal aggregates are sometimes found.

EMERSED LEAVES.

The emersed leaves are oblong to lanceoplate sharply or even laciniately toothed, and the intermediate ones between the aquatic more or less cleft or lobed. In structure they are bifacial. A surface view of the epidermis of the upper face is more regular or rather less irregular in cell structure (Fig. 14). The stomata are smaller than those of the lower face and orbicular whereas below they are slightly larger and oval. (Fig. 15). The chlorenchyma viewed from the lower face has many intercellular spaces (Fig. 16). It changes in shape gradually as it passes inwards to the two layers of palisade chlorenchyma. Nearer the midrib the palisade as well as the chlorenchyma pass gradually into rounder chlorophylless cells on both faces. This is augmented by two layers of thick walled cells (Collenchyma) on the lower face and a wedge of similar stereome on the other face. Sectioned about the middle of the leaf there is a large central collateral bundle with several lateral ones in a semicircle (Figs. 17 and 18). In the petiole or at the base of the leaf these are coalesced into one large semicircular collateral bundle. Opposite to the phloem strand and immediately under the stereome on the lower face.

The characteristic features of the plant are the very simple wood bundles undergoing scarcely any secondary changes, as also the simplicity and regularity of all the structures. The roots are in the adult stage of the plant all adventitious and develop chlorophyll regularly as far as the stele. The stomata of both faces of the leaves are somewhat different and the extrastelar cells of the aquatic foliage exclusive of the epidermis have very characteristic scalariform markings. The aquatic foliage is as typically centric in type as the aerial leaves are bifacial.

EXPLANATION OF THE FIGURES.

Fig. 1.—Cross section of the young root of *Megalodonta Beckii*. (*a*) cortical intercellular spaces, (*b*) smaller spaces, (*c*) endodermis, (*d*) pericycle, (*e*) phloem (leptome), (*f*) xylem (hadrome), (*g*) pith, (*h*) latex tube.

Fig. 2. Cross section of the epidermis (ep) and hypodermis (hy) of an older root. (co) cortical chlorenchyma.

Fig. 3. Structure of a latex tube in an older root showing the arrangement of the secreting cells.

Fig. 4. Longitudinal section through the central part of an older root. (*a*) epidermis, (*b*) hypodermis, (*c*) cortical parenchyma with chlorophyll, (*d*) intercellular space, (*e*) extrastelar fundamental tissue the outer cells with chlorophyll, (*f*) endodermis, (*g*) pericycle, (*h*) secretion cells with a latex tube between them, (*i*) phloem, (*l*) wood parenchyma between the protoxylem and inner metaxylem.

Fig. 5. Cross section of a secton of the stele of the rhizome. (*sp*) cortical intercellular space, (*co*) cortex cells, (*la*) latex tube, (*st*) stereome outside of the phloem of the fibrovascular bundle (mestome), (*ca*) Cambium, (*pi*) pith.

Fig. 6. Cross section showing the arrangement of the bundles in the stem of the same. The xylem is endarch pentarch.

Fig. 7. Cross section of the stem (floating, showing the arrangement of the bundles. Figs. 6 and 7 diagramatic and magnified about 18 diameters.)

Fig. 8.—Cross section of the floating equatic stem showing (*e*) epidermis with cortex beneath in which are the latex tubes (*la*) and the large intercellular spaces (*sp*) farther in the stele with the collateral bundles and the outwardly bulging pith (Medullary rays) (*m*), the central pith (*pi*), (xy^1) the protoxylem and (xy^2) the mataxylem.

Fig. 9. Cross section of medium sized division of the aquatic leaf a little above the middle, showing the outer layer of epidermis with chlorophyll and the inner mesophyll also with chlorophyll. In the centre is the single fibrovascular bundle with a few xylem and phloem elements also a latex tube.

Fig. 10. One of the larger mesophyll cells of the above teased out to show markings of the cell wall.

Fig. 11. Single fibrovasular bundle of a larger division near the base of petiole. (*ph*) phloem and (*xy*) xylem. (*wp*) wood parenchyma, and (*me*) mesophyll.

Fig. 12. View of the epidermis of the aquatic leaf divisions.

Fig. 13. Cross section of the bundle of the aquatic leaf petiole with bundle of (*xy*) xylem and (*ph*) phloem, (*gl*) latex tube, (*cr*) crystal aggregate of calcium oxalate.

Fig. 14. Epidermis of the upper face of the aerial leaf with stomata.

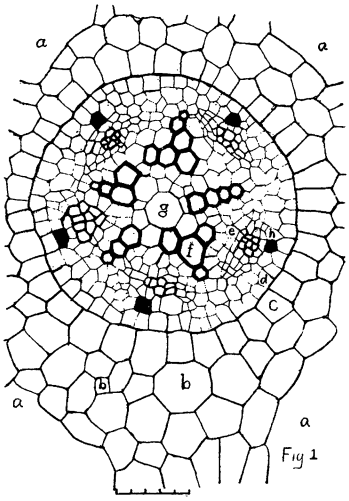
Fig. 15. Epidermis of the lower face of the aerial leaf showing stomata.

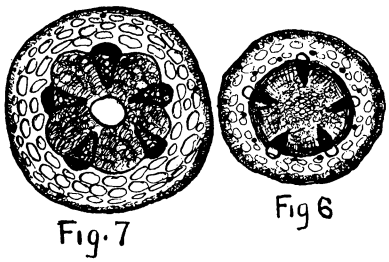
Fig. 16. View of the pneumatic tissue under the epidermis of the lower face of the emersed leaf.

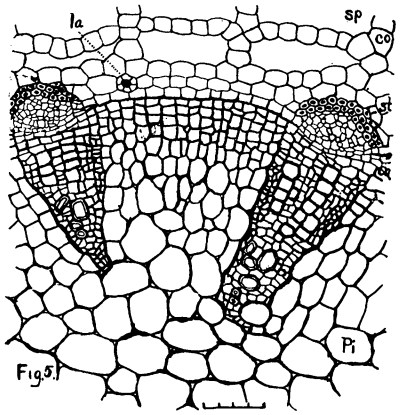
Fig. 17. Cross section of the middle part of an aerial leaf at the midrib (*ep*) lower epidermis with collenchyma or thick angled cells within it, (*c*), (*co*) fundamental tissue, (*ph*) phloem and (*xy*) xylem of the collateral bundles, (*pl*) modified palisade chlorenchyma.

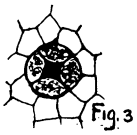
Fig. 18. Cross section of an emersed leaf showing the arrangement of (*ep*) the lower epidermis, (*chl*) pneumatic chlorenchyma, (*pa*) palisade chlorenchyma, (*st*) stomata.

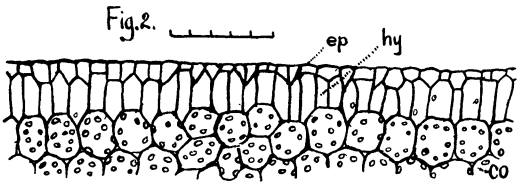
Scale of all the drawings: one division equals 12.5 microns.











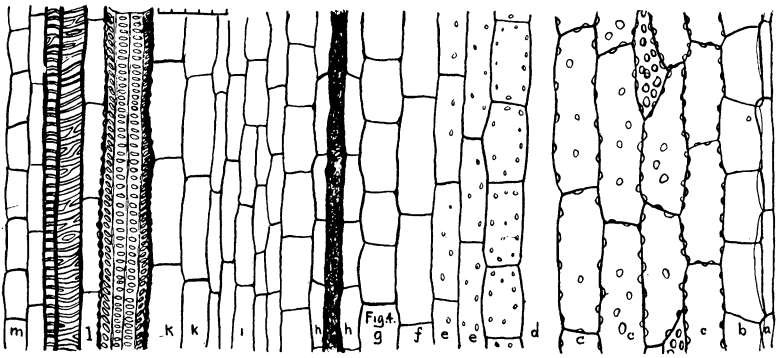


Plate XI. HOECK on ANATOMY OF MEGALODONTA BECKII.

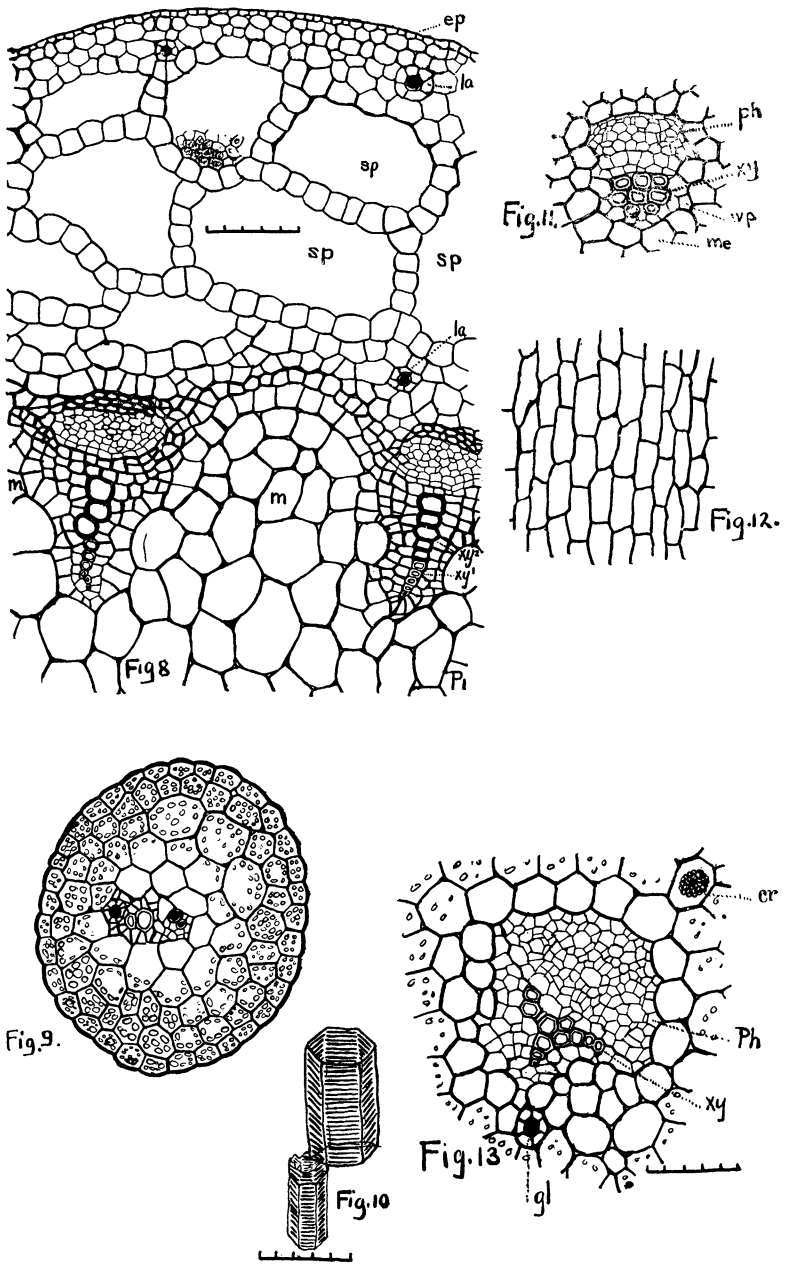
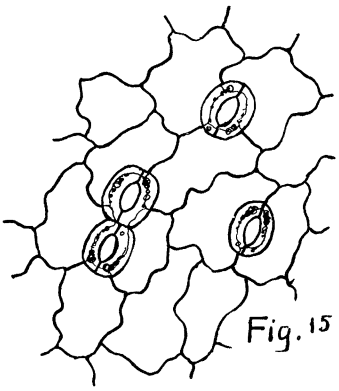
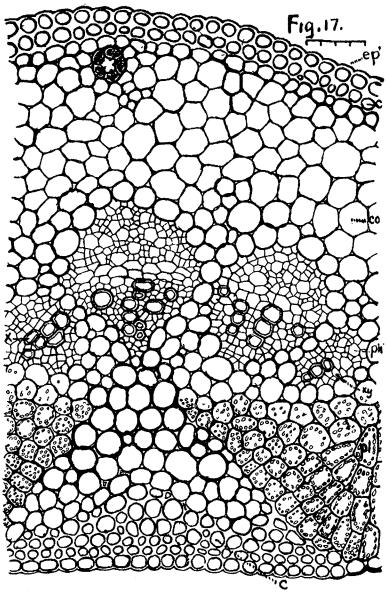
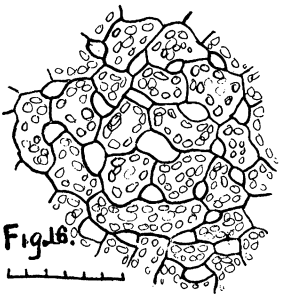
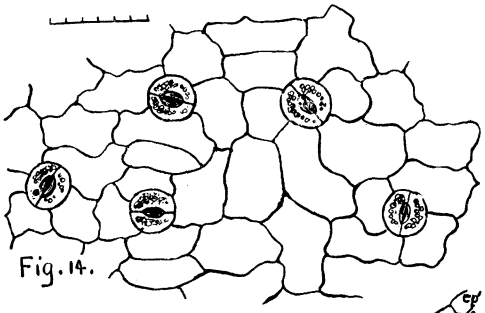


Plate XII. HOECK on ANATOMY OF MEGALODONTA BECKII.









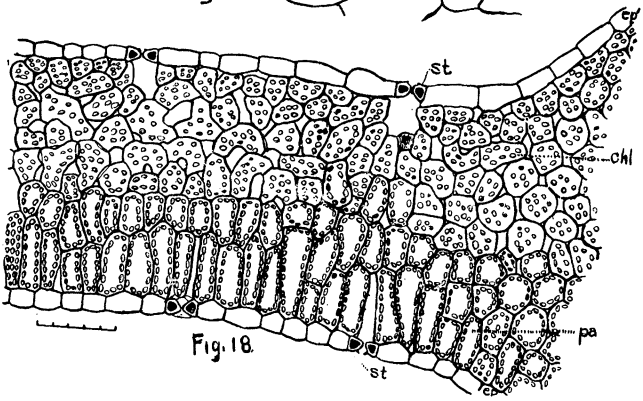


Plate XIII. HOECK on ANATOMY OF MEGALODONTA BECKII.